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LOCAL DISTRIBUTION AND INTERSPECIES INTERACTIONS IN MICROTINES, GRAND TETON NATIONAL PARK, WYOMING

Tim W. Clark[1]

Abstract.— Some ecological relationships and interspecies interactions (i.e., habitat, foods, and reproduction) between *Microtus pennsylvanicus pullatus*, *M. montanus nanus*, *M. longicaudus mordex*, and *Clethrionomys gapperi galei* were investigated in Grand Teton National Park, Wyoming. Trapping was conducted from June-July, 1968 and May-July, 1969 yielding 110 *M.p.p.*, 171 *M.m.n.*, 17 *M.l.n.* and 41 *C.g.g.* Six plant communities were defined structurally; all communities contained voles but varied considerably in numbers of species and individuals. Analyses of stomach contents showed similar diets. Embryo counts indicated that there was no significant interspecies differences in litter sizes. Females of all species were pregnant in about equal proportions. Almost all adult males showed descended testes and were reproductively active. Testicular and seminal vesicle weights and lengths fluctuated. *M.p.p.* mean body weights were largest: M44.7g (N=31), F38.1g (N=29); this was nearly twice the mean weights of *C.g.g.*: M20.4g (N=7), F23.3g (N=3). Weights for *M.m.n.* and *M.l.m.* fell between these extremes and were similar to each other. Trends in differential habitat use were clearly demonstrated and evidence suggests the four microtines are at least partially incompatible.

Four common rodents in Grand Teton National Park are: *Microtus pennsylvanicus pullatus* (meadow vole), *M. montanus nanus* (mountain vole), *M. longicaudus mordex* (long-tailed vole), and *Clethrionomys gapperi galei* (red-backed vole). Except for Findley (1951 and 1954), Negus and Findley (1959), and Stoecker (1970), little is known on distributions and ecology of these four species in the park. It is well documented that population levels are directly linked with relative numbers of other species in the community (Wirtz and Pearson, 1960; Curry-Lindahl, 1959; DeLong, 1966; Lidicker, 1966; Whitaker, 1967; Batzli, 1968; Shure, 1970). This paper further elucidates some ecological relationships and interspecies interactions (i.e., habitat, food habits, and reproductive characteristics) between these microtines in Grand Teton National Park, Wyoming.

Methods

The study was conducted in June and July, 1968, and May through July, 1969. A total of 339 specimens were collected: 171

[1]Department of Zoology, University of Wisconsin, Madison 53706.

Microtus montanus, 110 *M. pennsylvanicus*, 17 *M. longicaudus*, and 41 *Clethrionomys gapperi*. Sherman live traps and snap traps were used, and each trapline (1 trap every 10 meters) was left for 3 to 6 days, then moved to a new site. Traplines ranged from 25 to 50 traps each. For each Sherman trapline set, two snap traplines were set in each community. Thus the relative proportion of live traps to snap traps was uniform between communities.

Table 1 summarizes the six lowland plant communities trapped to determine habitat affinities. More detailed descriptions are given by Clark (1971) and Reed (1952).

Food uses were ascertained by stomach content examination. Contents were identified and a volumetric estimate made to the nearest 5 percent for each item. The mean volumetric estimates and frequencies of occurrence of each item were calculated (Clark, 1968).

In the field, all males were checked for position of testes; females were examined for condition of mammae (relative prominence and possible lactation). In the laboratory, male reproductive systems were removed; testes and seminal vesicles were examined, weighed, and measured. In the females, the number of embryos was counted.

Table 1. Comparison of plant communities sampled for microtines in Grand Teton National Park, Wyoming.

Plant Community	Prominent Species	Characteristics
1. Sedge-Meadow	*Carex* spp. *Aleopecurus aequalis* *Hordeum bachyantherum*	Underlain by firm sod; often covered with several cm of water; no woody plants, only sedges, grasses, and forbs
2. Sedge-Grass Meadow	*Carex* spp. *Agropyron trachycaulum* *Bromus, Poa, Agrostis*	Slightly elevated ground: very productive, 30 spp. of forbs; no woody plants, only sedges, grasses, and forbs; rarely covered by water
3. Shrub-Swamp	*Salix* sp. *Bromus, Poa, Calamagrostis, Aster, Aconitum, Castelleja, Ranunculus*	Water table near surface; stable; reduced light intensity under shrubs along with increased moisture; woody plants-shrubs, sedges, grasses, and forbs; shrubs over 50 percent ground cover
4. Shrub-Sedge-Grass Savanna	Same as (3) above	Shrubs less than 50 percent ground cover
5. Aspen	*Populus, Aster, Helianthella, Lupinus*	More level sites adjacent to swamps and meadows; closed tree canopy, dense shade; soil moist in spring but diminishes in summer
6. Big Sagebrush	*Artemisia*, spp., *Purshia* *Stipa, Poa, Bromus, Aster, Eriogonum, Potentilla*	Most widespread and conspicuous community; shrubs, forbs, and grasses; very dry, little to no water

Measurements of tail, hind foot, and total lengths and body weights were taken on all specimens. All *M. pennsylvanicus* and *M. montanus* were identified on the basis of molar structure. Representative specimens were prepared as museum skins and deposited in the Jackson Hole Biological Research Station collection and in the Museum of Natural History, University of Wisconsin-Stevens Point.

Results

Habitat affinities.— Habitat affinities were based on the plant communities in which capture per species was greatest (Maxell and Brown, 1968). All communities contained voles but varied considerably in numbers of species and individuals (Figure 1). Two communities (Sedge-Meadow and Sedge-Grass Meadow) were exclusively occupied by *M. montanus*, while the other four communities showed multispecies occupancy. The Big Sagebrush Community yielded only two species (*M. montanus* and *M. pennsylvanicus*), the Shrub-Swamp Community three species (all but *M. longicaudus*), and the Shrub-Sedge-Grass Savanna and Aspen Communities all four microtine species.

M. montanus was found in all six plant communities, its population numbers exceeding *M. pennsylvanicus* (the second most abundant species) in all communities except the Shrub-Swamp, where *M. pennsylvanicus* greatly outnumbered other voles. *M. pennsylvanicus* showed the second widest distribution in four communities. *Clethrionomys gapperi* occupied three plant communities and *M. longicaudus* only two (Figure 1).

Five of the six plant communities (excluding Big Sagebrush) are in successional sequence on the wetter sites in Jackson Hole (Reed, 1952). Some general characteristics of these communities in relation to vole distribution are given in Figure 1. The closer the plant community to climax, the greater the vole species diversity [species diversity refers to the number of species in each community (M'Closkey, 1972)]; correlated to this is a trend toward mesic soil-moisture conditions and more complex plant community structure (i.e., potentially more niches). The Aspen Community, the highest seral community of the sequence, possessing mesic soil-moisture conditions and three vegetative strata (herbs, shrubs, and trees), contained all four microtines. The simpler the community structurally—by virtue of its early successional position (Sedge-Meadow or Sedge-Grass Meadow) or limited moisture (Big Sagebrush)—the smaller the species diversity, one and two species, respectively.

However, the greatest species diversity was not correlated with greatest total populations numbers. The Shrub-Swamp Community is characterized by only two vegetational strata (herbs and shrubs), a 50-100 percent ground cover of shrubs, and some areas inundated by several cm of standing water; it is located near the middle of the successional sequence. It was this community that showed the greatest absolute numbers of voles (N=117) and the greatest CI,

	Herbs	Herbs	Shrubs Herbs	Shrubs Herbs	Trees Shrubs Herbs	Shrubs Herbs
	Wet - Moist		Wet	Moist		Dry
	Generalized Hydrosene Succession					
Microtus longicaudus				0.1 (N=2)	0.7 (N=15)	
Clethrionomys gapperi			1.8 (N=26)	0.1 (N=2)	0.6 (N=13)	
Microtus pennsylvanicus			6.5 (N=90)	0.7 (N=11)	0.3 (N=7)	0.1 (N=2)
Microtus montanus	3.1 (N=53)	3.5 (N=60)	0.1 (N=1)	1.8 (N=30)	0.7 (N=16)	0.7 (N=11)
	Sedge-Meadow (1,704)	Sedge-Grass Meadow (1,595)	Shrub-Swamp (1,380)	Shrub-Sedge-Grass Savanna (1,653)	Aspen (2,071)	Big Sagebrush (1,633)
	PLANT COMMUNITIES					

Fig. 1. Distribution of some microtines in Grand Teton National Park, Wyoming, in relation to plant communities and their characteristics. Numbers in blocks are capture indices (i.e., captures per 100 trap days) and those below plant community names are trap days.

with almost twice the total catch as the second highest community (N=60). Nearly all voles in this community were *M. pennsylvanicus*. Population numbers were more or less comparable among the Sedge-Meadow, Sedge-Grass Meadow, Shrub-Sedge-Grass Savanna, and Aspen Communities, with a CI (captures per 100 trap days) of .031, .037, .027, and .025, respectively. The Big Sagebrush Community, a dry community, showed the lowest total population number (N=13) and a CI of only .008, over 90 percent lower than the most populous community (Shrub-Swamp, with N=117).

In the two communities where *M. montanus* was most abundant, other species were absent. The community where *M. montanus* was almost totally absent was the community showing the largest numbers of both *M. pennsylvanicus* and *C. gapperi*. The *C. gapperi* were situated on drier sites in peripheral areas of this community, and *M. pennsylvanicus* tended to occupy wetter areas. The driest community yielded two species, with *M. montanus* outnumbering *M. pennsylvanicus* seven to one. In the two communities containing all four microtines, the numbers of all species were considerably less than in communities that were occupied by only one, two, or three species. In all six communities, for every 10 *M. montanus* taken, 7.5 *M. pennsylvanicus*, 2.5 *C. gapperi*, and 1 *M. longicaudus* were captured.

Stomach contents.— Among the more obvious possibilities for competition between species is maintenance of adequate levels of energy and nutrition for meeting metabolic requirements. Analyses of stomach contents showed a similar diet in the four microtines (Table 2). Green plant materials comprised the major identifiable items in all stomachs; seed fragments were the other important food. The herbivorous habits of all species suggest potential competition for food, at least during seasons when food may be scarce. During the months of this study, food was abundant and did not seem to influence distributions.

Microtus montanus and *M. pennsylvanicus*, the two species probably most directly in competition, showed comparable levels of

Table 2. Comparative stomach contents of some microtines in Grand Teton National Park, Wyoming. Figures are mean volumetric estimates calculated to the nearest 1 percent; figures in parentheses are percent frequencies of occurrence; T indicates trace.

Stomach Contents	*Microtus montanus* (N=139)	*Microtus pennsylvanicus* (N=107)	*Microtus longicaudus* (N=14)	*Clethrionomys gapperi* (N=25)
Green plant materials	63(80)	94(80)	38(55)	59(76)
Seed fragments	8(13)	1(9)	1(1)	9(19)
Arthropods	T(1)			
Parasitic roundworms	4(8)	2(6)		
Hair				6(18)
Unidentified	25(100)	3(100)	61(100)	26(100)

parasitic roundworm infestations. Both *M. longicaudus* and *Clethrionomys gapperi* lacked worms. The infested voles otherwise looked healthy; the parasitic load did not seem to be responsible for any observable mortality.

Reproduction.— Differential reproduction may greatly enhance the competitive advantage of one species over another. The breeding status of females of the four microtine species is given in Table 3. Embryo counts indicated that there was no significant interspecies difference in litter sizes. The percentage of pregnant adult females in all species was similar except for *Clethrionomys gapperi*, which showed a pregnancy rate about one-half that of the other three. Throughout May, June, and July, females of all species were pregnant in about equal proportions, indicating continuous breeding activity of the population during this time.

Almost all adult males of the four species showed descended testes; males with scrotal testes are frequently used as an indication of population breeding (Packard, 1968). The mean testicular lengths and weights and mean seminal vesicle lengths and weights varied over the periods of study for all four species (Tables 4 and 5). Figure 2 shows testis lengths in millimeters and weights in milligrams for the four microtines. A sharp increase in lengths and weights was evident in *Microtus montanus* from June 16 to 30, corresponding to a slight decrease in the other three species. The relationship was not clear. In the other three microtines, testes parameters were more or less stable, showing no such sudden increase or decrease. Seminal vesicles showed a pattern of weights and lengths corresponding with that of testicular weights and lengths (Figure 2). The mean seminal vesicle parameters for *M. montanus* again increased sharply in late June, corresponding to the increase in testes size. The mean seminal vesicle length in *M. longicaudus* increased slightly during the same period (June 16-30), but a concomitant increase in seminal vesicle weights was absent. Testicular and seminal vesicle characteristics in *C. gapperi* showed no peak of activity, perhaps indicating a constant level of spermatogenic activity.

Morphological characteristics.— Relative body size may be significant in determining the outcome of agonistic interactions and, thus, species distributions. The four microtines varied in morphological characteristics (Table 6). *Microtus pennsylvanicus* mean weights were largest: males 44.7 g, females 38.1 g; this was nearly

Table 3. Comparative female reproductive statuses of four microtines, Grand Teton National Park, Wyoming.

Reproductive Characteristic	*Microtus montanus*	*Microtus pennsylvanicus*	*Microtus longicaudus*	*Clethrionomys gapperi*
Total number examined	50	46	4	11
Number pregnant	40	32	3	4
Mean number of embryos	6.35	6.59	6.00	6.00
Range in embryo number	4-9	4-9	5-7	4-7
Standard deviation	±1.29	±1.34	±1.16	±1.19

TABLE 4. Testis weights in mg and testis lengths in mm for four microtine species in Grand Teton National Park, Wyoming.

Periods	N	Mean	Range	S.D.	Mean	Range	S.D.
	Testis Weights (mg)				Testis Lengths (mm)		
			Microtus montanus				
May 15-31	6	680	526-729	±124	13.0	9-15	±2.86
June 1-15	7	535	261-676	±101	10.8	9-12	±0.80
June 16-30	11	1449	850-1818	±420	15.7	13-18	±2.06
July 1-15	9	535	500-570	± 35	10.7	10-12	±0.50
July 16-31	12	586	497-621	±321	11.8	9-14	±1.26
Total	45						
			Microtus pennsylvanicus				
May 15-31	10	1225	731-1185	±159	15.1	13-17	±1.27
June 1-15	10	1389	568-1849	±322	15.7	11-18	±1.81
June 16-30	7	6274	967-1501	±173	14.0	13-16	±1.73
July 1-15	8	1275	1060-1495	±178	15.0	14-17	±1.22
July 16-31	11	1190	1136-1238	±192	14.8	13-16	±1.64
Total	46						
			Microtus longicaudus				
May 15-31	3	541	436-582	± 89	12.0	11-13	±1.0
June 1-15	3	679	610-694	± 47	12.0	11-13	±1.0
June 16-30	4	535	489-569	±110	10.0	9-11	±0.8
July 1-15	4	587	502-621	±126	10.0	9-11	±0.8
July 16-31	1	610	—	—	11.0	—	—
Total	15						
			Clethrionomys gapperi				
May 15-31	4	364	330-380	± 23	9.7	9-10	±0.50
June 1-15	3	366	287-410	±218	10.0	—	—
June 16-30	5	409	362-440	±167	9.2	8-11	±1.09
July 1-15	5	318	289-354	±148	10.6	10-12	±0.89
July 16-31	3	392	—	—	9.3	9-10	±0.57
Total	20						

twice the mean weights of *Clethrionomys gapperi:* males 20.4 g, females 23.3 g. Weights for *M. montanus* and *M. longicaudus* fell between these extremes and were similar to each other.

The linear measurements of *C. gapperi* and *M. montanus* were similar, both smaller than the other two microtines. Even though *M. pennsylvanicus* had the largest body weight, its length was exceeded by that of *M. longicaudus. M. longicaudus* total and tail lengths are greatly expanded by its disproportionately long tail.

DISCUSSION

Animal distributions are influenced by a constellation of factors ranging from a complex of abiotic environmental gradients to biotic regulators including diseases, predators, and intra- and interspecific competition. The importance of these factors varies from area to area; it is difficult to dissect out each factor and determine its relative influence in controlling population distributions and numbers. This study examined some aspects of the environment as well as the relationship of other species in the community to distributions of some microtines. Distribution patterns suggest that some mecha-

Table 5. Seminal vesicle weights in mg and lengths in mm for four microtine species in Grand Teton National Park, Wyoming..

Periods	Seminal Vesicle Weights (mg)				Seminal Vesicle Lengths (mm)		
	N	Mean	Range	S.D.	Mean	Range	S.D.
			Microtus montanus				
May 15-31	6	379	286-399	± 69	19.0	14-22	±1.97
June 1-15	7	359	262-420	± 73	16.3	14-19	±1.38
June 16-30	11	824	270-1153	± 89	23.7	15-29	±6.18
July 1-15	9	364	287-435	± 61	17.2	14-20	±2.54
July 16-31	12	342	268-411	± 89	18.2	14-21	±3.16
Total	45						
			Microtus pennsylvanicus				
May 15-31	10	484	325-760	±118	20.1	17-24	±1.89
June 1-15	10	733	316-1210	±281	22.1	14-26	±3.45
June 16-30	7	623	410-875	±179	20.5	17-23	±2.51
July 1-15	8	936	561-1420	±357	20.5	17-24	±2.89
July 16-31	11	782	528-926	±286	20.7	17-22	±2.44
Total	46						
			Microtus longicaudus				
May 15-31	3	340	289-390	± 51	12.3	11-14	±1.53
June 1-15	3	205	176-256	± 44	14.0	13-15	±1.00
June 16-30	4	240	210-314	± 94	17.0	14-18	±2.00
July 1-15	4	320	286-354	± 72	14.0	13-16	±1.41
July 16-31	1	280	—	—	14.8	—	—
Total	15						
			Clethrionomys gapperi				
May 15-31	4	230	100-251	± 62	16.0	14-17	±1.50
June 1-15	3	235	140-252	± 72	15.0	14-16	±1.00
June 16-30	5	210	126-246	±117	15.4	15-16	±0.55
July 1-15	5	279	224-343	± 69	14.6	13-17	±1.52
July 16-31	3	261	242-289	± 24	16.0	15-17	±1.00
Total	20						

nism of active separation is operative, especially between *Microtus montanus* and *M. pennsylvanicus*. Some of the habitats contained multiple species, while others only one. In the habitats containing one species, interspecific relations may be a factor keeping other species out. In situations where two or more species occur, competition is probably occurring. As discussed by Whitaker (1967) when competition is great enough one or both species may tend to reduce the population of the other species. Then we would expect to find lower population numbers in areas where both species occur than in situations where only one species is found. Grant (1970a) concluded from a series of laboratory studies supported by fieldwork (Grant, 1969, 1970b) that when adults of two species that normally occupy different habitats in mainland regions meet in the wild they will interact aggressively and tend to disperse. This habitat segregation is maintained on islands where both genera *(Clethrionomys* and *Microtus)* are represented by at least one species; but on islands where only a single species of one of the genera occurs, it often occupies the habitat of the absent genera (Ota and Jameson, 1961;

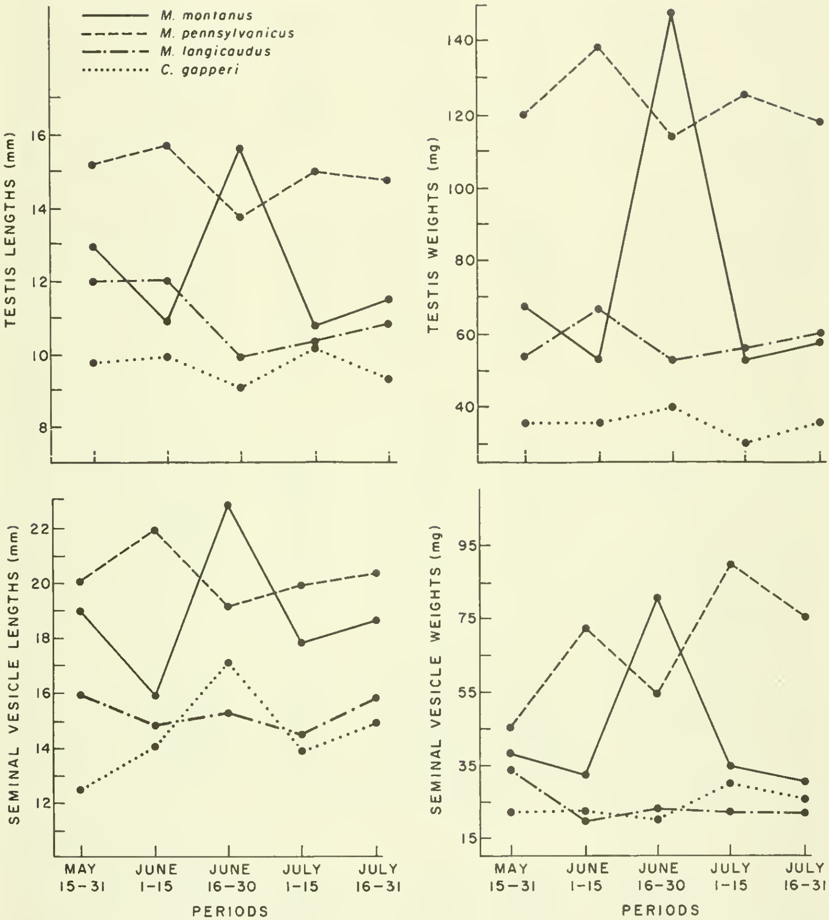

Fig. 2. Changes in testis lengths (mm) and weights (mg) and seminal vesicle lengths (mm) and weights (mg) for four microtines, Grand Teton National Park, Wyoming.

Cameron, 1964; Corbet, 1964). This implies some form of population interaction in areas of sympatry.

Ecological segregation in my study could be a result of each species responding to microenvironmental requirements and may not be related to other species in the community. Whereas several of the plant communities sampled in this study are very similar and since the four microtines are closely related taxonomically, it is likely that they share some similar ecological requirements; therefore, distributions exhibited are probably the result of competition for these requirements. When few or no ecological differences are present between two or more species occurring together, and

TABLE 6. Comparison of body lengths in mm and body weight in gm between four microtines, Grant Teton National Park, Wyoming.

	Morphological Characters				
Species	Total Length X Range	Tail Length X Range	Ear Length X Range	Hind Foot Length X Range	Body Weights X Range
Microtus pennsylvanicus					
♂ (N=31)	165.27(150-183)	40.69(15-47)	14.63(12-17)	19.63(17-22)	44.74(35-55)
♀ (N=29)	158.48(143-185)	40.41(34-47)	13.50(12-15)	18.31(17-20)	38.10(31-59)
Microtus montanus					
♂ (N=17)	148.31(99-176)	36.81(24-46)	13.56(10-16)	18.94(16-21)	34.58(31-54)
♀ (N=20)	152.11(144-164)	39.00(30-47)	13.16(12-15)	18.55(17-20)	34.58(26-51)
Microtus longicaudus					
♂ (N= 3)	184.30(169-199)	63.00(57-67)	16.00(15-18)	19.00(18-20)	34.00(30-39)
♀ (N= 1)	185.00 (0)	67.00 (0)	15.00 (0)	21.00 (0)	34.00 (0)
Clethrionomys gapperi					
♂ (N= 7)	142.29(133-155)	40.29(33-43)	15.14(12-17)	17.14(16-18)	20.40(20-21)
♀ (N= 3)	147.00(145-149)	40.50(38-43)	15.00(15-—)	18.50(18-19)	23.30(19-28)

when species numbers are much lower than expected, the species may be adversely affecting one another (Whitaker, 1967) as is suggested by this study.

M. montanus occupied a wide range of plant communities and seems capable of existing in large numbers in all of them (with one exception) regardless of the other species present. Competitive interactions seem to be occurring with *M. pennsylvanicus*, resulting in the restriction or total elimination of *M. pennsylvanicus* from certain situations. Murie (1969) and Hodgson (1972) showed that *M. pennsylvanicus* demonstrated a wet substrate preference while *M. montanus* did not. In my study, *M. pennsylvanicus* occurred in largest numbers in the wettest situations and was present in limited numbers or totally absent from areas tending to the drier end of the spectrum. This concurs with Findley (1951, 1954) who concluded: (1) that where the range of *M. pennsylvanicus* overlaps that of *M. montanus*, a species well adapted to dry mountain grasslands, *M. pennsylvanicus* is forced to retire to its optimum niche, the hydrosere community, and (2) that the distribution of *M. pennsylvanicus*, in part at least, is due to competition with closely related microtines.

The relationships of *M. longicaudus* and *C. gapperi* are less clear; *M. longicaudus* is the most restricted of the four microtines. It is apparently capable of coexisting with the other three species, being found in the wetter, more structurally complex plant communities. A similar tendency was exhibited by *C. gapperi*, but it is capable of occupying a slightly wider latitude of situations. Voles of the genera *Clethrionomys* and *Microtus* tend to occupy different habitats, the former woodlands and the latter grasslands (Hall and Kelson, 1959; Southern, 1964). Evidence that *M. pennsylvanicus* and *C. gapperi* tend to inhibit each other from using the opposite species habitat is abundant (Grant, 1969; Morris, 1969; Iverson and Turner, 1972).

Results of my stomach analyses suggest a similarity in food uses, but microtine populations seldom critically deplete their food supplies (Negus and Pinter, 1966). The quality, rather than the quantity, of available food was shown to exert considerable influence on initiation, duration, and success of the breeding season in natural populations of *M. montanus* (Negus and Pinter, 1966). A comparative reproductive investigation showed litter sizes among the four microtines to be similar, with no species having a disadvantage in this respect, except possibly *C. gapperi*, which showed about one-half the pregnancy rate of the other three microtines. This low numerical productivity may be offset by a greater survivorship, or the population may suffer suppression by the superior numbers produced by the other three species. However, the latter probably was not the case, as suggested by the wider latitude of occupancy of plant communities than *M. longicaudus*, which showed greater productivity.

Even though litter sizes are comparable, the first species coming into breeding in the spring would have an advantage, especially if the females establish a breeding territory excluding all other species as suggested by Stoecker (1970). Over the three months of this study, nearly the entire adult populations of all four microtines were in breeding condition.

Other factors that may be involved in segregation are behavioral interactions (Murie, 1963; Stoecker, 1970) and possible physiological differences in water balance (Getz, 1963). Stoecker (1970), in an analysis of sympatry in *M. pennsylvanicus* and *M. montanus*, found that because of co-occurrence in the same situations and because of the similarity in their time of activity, behavioral contacts unquestionably occur. He found *M. montanus* to agonistically dominate *M. pennsylvanicus*. Social intolerance between the two species was further suggested by the low recruitment of young and by immigration of one species when the other was removed by trapping. Stoecker's (1970) results contrast with those of Grant (1970a), who noted that the outcome of interspecies encounters depends on where and when they occur and upon the relative body sizes of the interactants (larger species almost always wins).

The existence of trends in differential habitat use was clearly demonstrated in this study, and evidence suggests that the four microtines are at least partially incompatible. However, a multiplicity of ecological and behavioral factors are probably operating synergistically to produce the observed species distributions.

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